



The Pleistocene non-hominid vertebrate ichnofossil record of Italy

Gian Luigi Pillola ^{1,*}, Maria Rita Palombo ², Adolfo Panarello ³, Daniel Zoboli ¹

¹ Dipartimento di Scienze Chimiche e Geologiche, Università di Cagliari, Cittadella Universitaria (Blocco A), Monserrato (CA), Italy

² Istituto di Geologia Ambientale e Geoingegneria (IGAG), Consiglio Nazionale delle Ricerche, Montelibretti (RM), Italy

³ Laboratorio di Ricerche Storiche e Archeologiche dell'Antichità, Dipartimento di Scienze Umane, Sociali e della Salute, Università di Cassino e del Lazio Meridionale, Cassino (FR), Italy

* Corresponding author: pillolag@unica.it

ABSTRACT - This work presents the current knowledge on the Quaternary vertebrate ichnological record (excluding the hominid data) of peninsular and insular Italy. In particular, the data concerning different Pleistocene localities of Sardinia (e.g. Capo Mannu and Funtana Morimonta) and the Middle Pleistocene Foresta “Devil’s Trails” ichnosite of Roccamonfina Volcano (Campania) are here discussed. In the Pleistocene record of Sardinia four ichnotaxa are known: *Bifidipes* aff. *B. aeolis* as regard the Early Pleistocene, and *Proboscipeda panfamilia* McNeil, Hills, Tolman, and Kooyman, 2007, *Bifidipes* isp. and *Canipeda* isp. as concerning the Middle-Late Pleistocene record. Four ichnotaxa are identified also in the Middle Pleistocene ichnosite of Foresta “Devil’s Trails”: *Proboscipeda panfamilia*, McNeil, Hills, Tolman, and Kooyman, 2007, *Ursichnus* isp., *Hippipeda* isp., and the ichnogenus *Pecoripeda* (? ichnosubgenus *Cervipeda*). The systematics of the mammal ichnofossils and the putative trackmakers are discussed and, furthermore, the ages, the stratigraphic and geological data are briefly treated to suggest the relative palaeoenvironmental contexts.

Keywords: Quaternary; palaeoichnology; mammals; Carnivora; Artiodactyla; Proboscidea; Sardinia; Campania.

Submitted: 2 February 2020-Accepted: 24 April 2020

1. INTRODUCTION

Tracks and trackways of vertebrates are relatively scarce in the Pleistocene record of Italy, especially if compared to the numerous coeval deposits rich in vertebrate fossils remains. Until now, only ichnofossils related to large mammals are reported in few localities on the Italian Peninsula and in several sites principally localized along the western coast of Sardinia.

As regard the record of the Italian Peninsula, ichnofossils left by large mammals (excluding hominid tracks and trackways) have been reported in aeolian-reworked alluvial sandsheet deposits of Upper Valdarno, Chianti area (Early Pleistocene), in late-glacial muddy cave floors (“Grotta del Fiume”, Marche and “Sala dei Misteri”, Liguria), and in Middle Pleistocene ignimbrite deposits of the north-eastern slope of the Roccamonfina Volcano, Campania (Ghinassi et al., 2013; Citton et al., 2017; Panarello et al., 2017b, 2020; Palombo et al., 2018).

The Sardinian ichnofossil record is related only to coastal and aeolian contexts instead (Fig. 1a). Indeed, during the Pleistocene glacial-phases, the ample western

continental shelf of Sardinia emerged due to the global sea level lowering, resulting in the extension of dune fields exposed to the NW glacial winds. This scenario led to the formation of a wide range of conservative environments, which allowed the preservation of the footprints left by large mammals (Fanelli et al., 2007; Kotsakis et al., 2008; Pillola and Zoboli, 2017; Zoboli and Pillola, 2018).

Therefore, we give mention of the Pleistocene Sardinian ichnosites and discuss the main ichnofossil record as well as the footprints of large mammals exposed in the Roccamonfina Volcano area (Fig. 1b).

2. QUATERNARY VERTEBRATE ICHNOFOSSILS OF SARDINIA

Until just over a couple of decades ago, there were few data concerning the palaeoichnology of Sardinian vertebrates and the only evidence was relegated to the Carboniferous record of the San Giorgio Basin, near Iglesias (Fondi, 1980; Marchetti et al., 2018). However, several studies have been made on the palaeoichnology of the Pleistocene Sardinian vertebrates and our knowledge

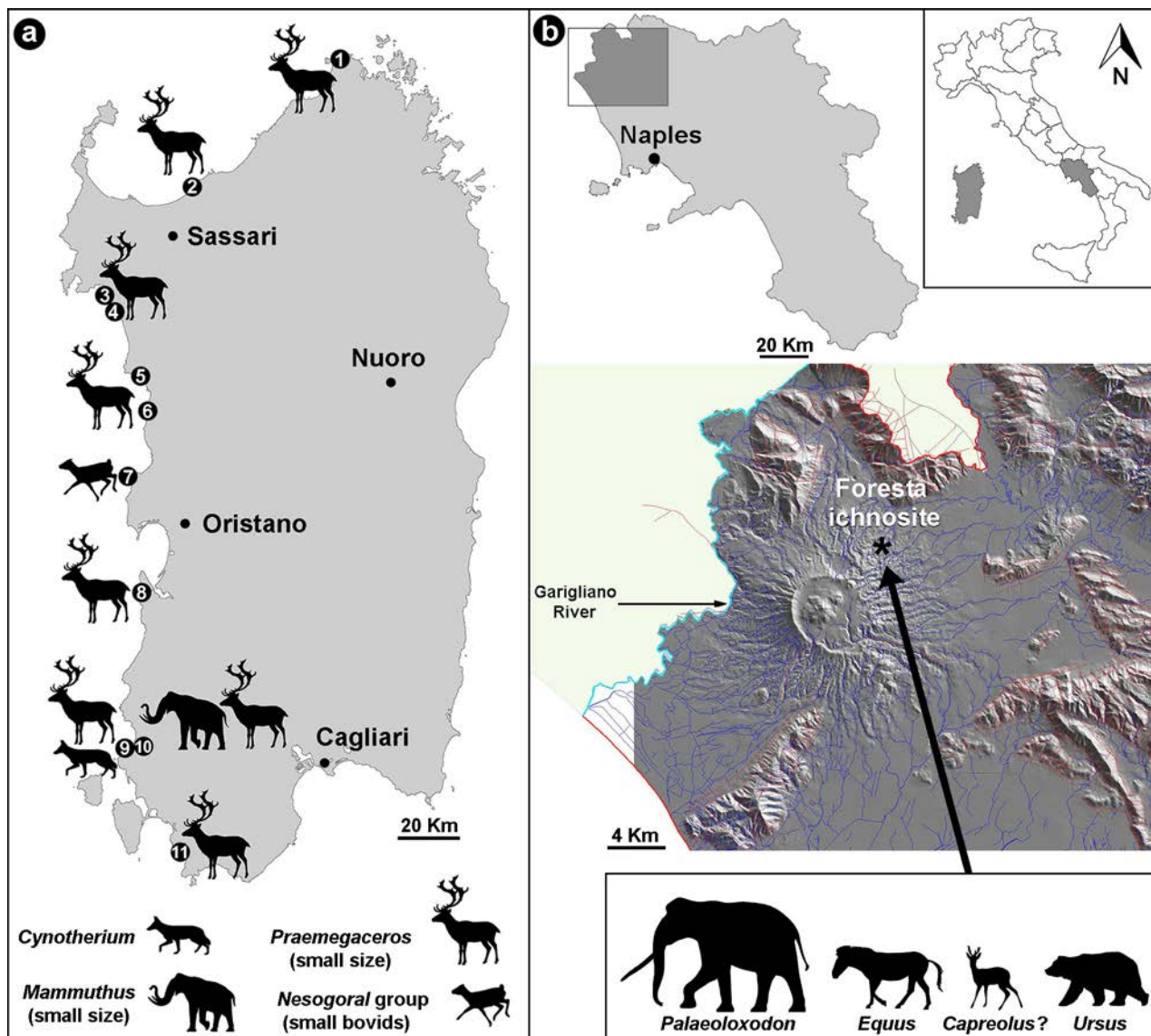


Fig. 1 - a) Location map showing Early-Late Pleistocene main ichnosites of Sardinia: 1, Santa Teresa di Gallura; 2, Punta Tramontana (Castelsardo); 3, Cala Bona (Alghero); 4, Il Cantaro (Alghero); 5, Torre Argentina (Bosa); 6, Torre Columbargia (Tresnuraghes); 7, Capo Mannu (San Vero Milis); 8, Pistis (Arbus); 9, Porto Paglia (Gonnesa); 10, Funtana Morimonta (Gonnesa); 11, Porto Pino (Sant'Anna Arresi); b) Location of the Foresta "Devil's Trails" ichnosite with the current geomorphology of the Roccamonfina Volcano, including the hydrographic framework and the main fault systems (Modified after © 2001-2012 Laboratory of Geomatics and Cartography (L.G.C.) of the Vesuvian Observatory (OV), Naples Section of the Institute National Geophysics and Volcanology - INGV).

has been considerably increased during the last years (Fanelli et al., 2007; Kotsakis et al., 2008; Pillola and Zoboli, 2017; Zoboli and Pillola, 2018).

In the course of the Quaternary, the western coast of Sardinia was characterized by important aeolian processes, which originated extensive dune systems. These deposits are generally associated with palaeosols, alluvial and fluvial deposits (Orrù and Ulzega, 1986; Andreucci et al., 2010). The age of the aeolian deposits was questioned and debated, and different generations of dunes along the western coast of the island have been recognized by several authors (e.g. Orrù and Ulzega, 1986; Andreucci et al., 2006; Lecca and Carboni, 2007; Abbazzi et al., 2008).

The vertebrate ichnofossils reported to date were found only in fossil aeolian deposits (s.l.) mainly localized along the northern and western coasts of the island, where numerous tracks and trackways of large mammals have been reported (Fanelli et al., 2007; Pillola and Zoboli, 2017).

2.1. BOVID FOOTPRINTS FROM THE EARLY PLEISTOCENE OF CAPO MANNU

A few small didactylous footprints have been noticed in an exposed section of the D6 dune unit, consisting of strongly cemented fine sandy layers, at the top of the Capo Mannu (Sinis Peninsula, W Sardinia) aeolian stratigraphic sequence during a geological survey made by two of us

(G.L.P. and M.R.P.) and some colleagues (Kotsakis et al., 2008). The tracks mainly occur in the distal part of the left side of the section, where the layer bedding surfaces are sub-horizontal or gently inclined (Figs. 2, 3).

2.1.1. Geological context

The over 80 m-thick stratigraphic succession exposed at Capo Mannu (Capo Mannu Formation, CMFm) attests to a regressive phase, lasted not less than 0.4-0.5 Ma, evolving from marine-littoral to continental-dunal deposits with interbedded palaeosols (Figs. 2, 3).

A detailed stratigraphic analysis of the Capo Mannu Fm was provided by Carboni and Lecca (1995). The

CMFm, separated from the underlying Middle Miocene-Messinian sequence by an erosional unconformity, consists of seven main dune units (D1-D7) (and nineteen dune subunits) separated by first-order boundaries. Three dune units (D5-D7) of lesser lateral continuity overlay the first four dune units (D1-D4). The sequence of dune units, from D2 to D7, shows a clear depositional continuity, whereas no clear stratigraphical conformity can be observed between the first dune unit D1 and the overlying second dune unit D2 because the contact is not exposed, but covered by Late Pleistocene deposits (from MIS 5 to MIS 2) (Carboni and Lecca, 1995; Abbazzi et al., 2008 and references therein).

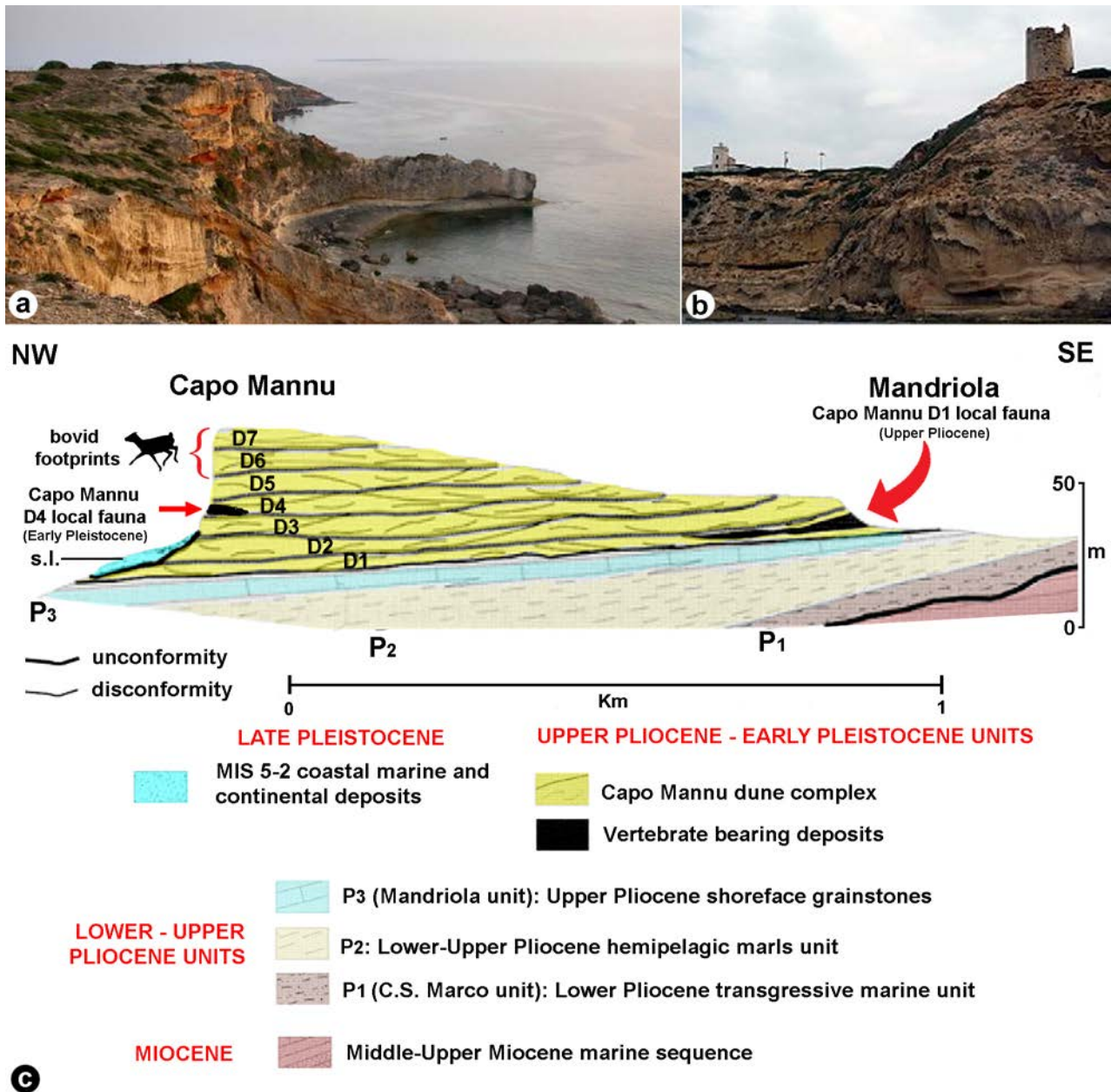


Fig. 2 - Capo Mannu (San Vero Milis municipality, central-western Sardinia). a) panoramic view the Sinis Peninsula (from Capo Mannu toward southeast); b) particular of the Capo Mannu dune complex; c) syntetical cross-section of stratigraphical units exposed at Capo Mannu promontory and location of dune units at Mandriola (D1) and Capo Mannu cliff (D2-D7 sedimentary succession) (modified from Abbazzi et al., 2008 and Palombo and Rozzi, 2014).



Fig. 3 - Bovid footprints of the Early Pleistocene aeolian deposits of Capo Mannu (central-western Sardinia). a) the main stratigraphical succession exposed on the Capo Mannu cliff; b) cemented aeolianites of D6 dune unit; c) cross section of sandstone showing footprint impressions and the deformation of the underlying laminas (modified from Kotsakis et al., 2008).

The entire Capu Mannu dune complex (D1 to D7) accumulated in the course of a period mainly characterized by hot and dry climatic conditions and intense aeolian dynamics, though cooler and wetter climatic conditions occurred during marine regressive eustatic phases (Carboni and Lecca, 1995; Abbazzi et al., 2008). Abbazzi et al. (2008) analyzed the sediments related to the climatic-eustatic cyclicity according to cyclical stratigraphical models. Results obtained by the Italian authors by correlating the 7 dune units with the orbital eccentricity cycle and the 19 subunits with precession or obliquity of earth axis, suggest that the sedimentation process lasted not less than 0.4-0.5 Ma and not more than 1 Ma, and may had completed either

shortly before or after the beginning of the Calabrian stage (roughly between 2 and 1.5 Ma), based on the chronology generally accepted for the D1 unit, recording the oldest Capo Mannu vertebrate fauna (Angelone and Kotsakis, 2001; Palombo, 2018a and reference therein).

The vertebrate remains were retrieved from the slightly developed red-brown sand-loam paleosols of Capo Mannu D1 dune unit exposed at Mandriola (Angelone and Kotsakis, 2001; Abbazzi et al., 2008; Palombo, 2009, 2018a). The presence of the slightly modified murid *Rhagapodemus azzarolii* in the Mandriola local fauna assemblage provides its best chronological constraint. Its continental ancestor was, indeed, *Rhagapodemus ballesioi*, a Ruscinian species of western and central

Europe which likely dispersed to Sardinia not earlier than the Zanclean/Piacenzian transition (Bruijn and Rümke, 1974; Angelone and Kotsakis, 2001), as probably nearly all the insectivores recorded at Mandriola did. Accordingly, the hypothesis that the age of the Capo Mannu D1 dune unit might be younger than MN 15 “zone” (Early Piacenzian?) seems to be the most plausible (see Palombo and Rozzi, 2014 for a discussion; Palombo, 2018a). The Mandriola local faunal assemblage belong to the Nesogoral Sardinian Faunal complex, in particular the oldest of the two Faunal sub-Complex it encompasses (i.e. Mandriola and Capo Figari-Orosei 1 FsC) (Palombo, 2009, 2018a).

A slightly younger vertebrate faunal assemblage (*Testudo pecorinii* Delfino, in Abbazzi et al., 2008; *Sus sondaari* van der Made, 1999; *Nesogoral* sp., Bovidae gen. et sp. indet., small-sized, Bovidae gen. et sp. indet., larger-sized) was present in the Capo Mannu D4 levels (Abbazzi et al., 2008). The presence of a suid showing morphological features closer to the type species from Capo Figari, apparently more advanced than those detectable in *Sus* aff. *S. sondaari* from Mandriola (van der Made, 1999; Abbazzi et al., 2008; Palombo et al., 2012a), as well as the diversification shown by the bovid remains, suggest that the faunal assemblage may be ascribed to the Capo Figari-Orosei 1 FsC (see Palombo and Rozzi, 2014 for a discussion).

2.1.2. The ichnofossil record

About thirty footprints were thus far detected in the Early Pleistocene (?Late Gelasian) aeolian sediments at the top of the stratigraphical sequence exposed on the cliff of Capo Mannu promontory, both in vertical sections and on bedding surfaces. The latter are badly preserved and difficult to identify because the tracks are either filled by overlapping sands or were made indistinct by erosive processes.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Bifidipes* Demathieu, Ginsburg, Guerin,
and Truc, 1984

Type Ichnospecies *Bifidipes velox* Demathieu,
Ginsburg, Guerin, and Truc, 1984

Bifidipes aff. *B. aeolis* Fornós, Bromley, Clemmensen,
and Rodríguez-Perea, 2002

(Fig. 3c)

The Capo Mannu footprints have not yet been studied in-depth and no photogrammetric models have been made to date. Therefore, here we report the results of some preliminary observations resulting from expeditious visual inspections made during two successive surveys, which enable us to describe only a few basic morphological traits.

In the less damaged tracks detected on bedding surfaces, the pad is somehow discernable, as an inflated disturbance zone asymmetrically developed, sometimes preserving hints of multiple, concentric sediment

dislocations.

The much more common tracks are those visible in vertical section (internal or oblique), arranged in slightly different oriented trackways, along the natural aeolian sediment sections exposed by erosion. In all the tracks, a strong deformation of the sedimentary laminae is clearly visible. Sometimes curved micro faults produce slightly displacements of laminae delimiting the zone that corresponds to the pad. The tracks corresponding to internal/nearly internal vertical sections show distinctly the insertion within the sediment of the forefoot (manus) and hindfoot (pes), moderately superimposed each other. Sometimes a hoof-like distal termination seems to be present.

The tracks impressed on the Capo Mannu dunal sediments by a small-sized artiodactyl are comparable in size with the tracks of *Bifidipes aeolis* left by *Myotragus balearicus* on similar substrates (Fornos et al., 2002). The only artiodactyls present at that time in Sardinia were the representatives of the genus *Nesogoral*, and, maybe, the smaller bovid *Asoletragus gentryi* (to date only known from an incomplete skull at Monte Tuttavista, Orosei) (Palombo et al., 2006, 2018a; Palombo et al., 2013). Accordingly, the hypothesis that the producer of Capo Mannu tracks was one among these endemic bovids seems to be the most rational.

The data available to date for the Capo Mannu footprints are, unfortunately, inadequate to evaluate the parameters crucial for understanding the gait of the trackmaker, such as the range of variation (if any) of the manus and pes prints relative positions and the length of stride, which depend on both the length and proportions of limbs and the speed of the type of gait (e.g. walking, trotting, running, jumping, etc.). Consequently, it is challenging to compare the tracks left by the quite long-legged, moderately cursorial Sardinian bovid (Rozzi and Palombo, 2013 and references therein) with those produced by the short-legged *Myotragus balearicus* with a low gear locomotion (Bover and Fornós, 2005).

2.1.3. Remarks

Demathieu et al. (1984) created the ichnogenus *Bifidipes* for artiodactyl “*Traces didactyles semblables à l’empreinte de deux sabots contigus. Les ‘pincés’, pointues en général, ont leurs bords toujours nettement séparés et divergents. A l’arrière, la séparation des ‘éponges’ n’est pas toujours nette. Quand l’empreinte est complète, la longueur dépasse toujours la largeur*” (Demathieu et al., 1984, p. 162). Since that time, the ichnogenic name frequently appeared in literature, although Vyalov (1966) had already created the ichnogenic name *Pecoripeda* for ruminant footprints (see also below section 3.1.2). In particular, Fornós et al. (2002, p. 308) provided an emended diagnosis for the genus and created the new ichnospecies *Bifidipes aeolis* for tracks and trackways left by *Myotragus balearicus* on aeolian deposits. The diagnosis of the new species (“*Bifidipes associated with considerable disturbance of the surrounding substrate including micro-folding and micro-*

faulting in aeolian sediments. Details vary with consistency and attitude of substrate surface. Pes may coincide with or fall behind manus. Stride irregular. Trackways commonly follow irregular course”) matches quite well some traits shown by the Capu Mannu footprints, which, like those of *Myotragus*, were left by an extinct endemic small-sized bovid walking on dunal aeolian deposits.

This is the reason why we decided to use the ichnogenetic name *Bifidipes*, although we are aware that it could be regarded of a junior synonym of *Pecoripeda*.

2.2. MAMMAL TRACKS AND TRACKWAYS FROM THE MIDDLE-LATE PLEISTOCENE OF SARDINIA

Tracks and trackways assigned to large mammals were recognized in pre- and post-Tyrrhenian aeolian deposits (s.l.) of several localities of Sardinia: Santa Teresa di Gallura, Punta Tramontana (Castelsardo), Cala Bona and Il Cantaro (Alghero), Torre Argentina (Bosa), Torre Columbargia (Tresnuraghes), Capo Mannu (San Vero Milis); Pistis (Arbus), Porto Paglia and Funtana Morimonta (Gonnesa), and Porto Pino (Sant’Anna Arresi) (Fanelli et al., 2007; Pillola and Zoboli, 2017; Zoboli and Pillola, 2018). The recorded ichnofossils are represented by isolated tracks and/or trackways left by proboscideans, megacerine deer and canids (Figs. 4, 5).

2.2.1. Geological context

Sedimentological and precise chronostratigraphic studies concerning the Sardinian localities are currently underway. However, a Middle-Late Pleistocene age has been generally assigned to the aeolian deposits (s.l.) of the western Sardinia on the basis of the relationships with the Tyrrhenian interglacial marine deposits (MIS 5e).

The geological settings of different sedimentary successions along the north and western coasts of the island show that aeolian deposits occur both below and above the MIS 5e deposits (Pecorini, 1954; Comaschi Caria, 1968; Carboni and Lecca, 1985; Kindler et al., 1997; Andreucci et al., 2006, 2010; Lecca and Carboni, 2007; Catto, 2010; Coltorti et al., 2010). The absence of the marine Tyrrhenian marker associated with aeolian deposits in the internal areas represents a problem for a precise chronological context.

As regard the Sulcis-Iglesiente area, where several ichnosites have been reported (Fanelli et al., 2007; Pillola and Zoboli, 2017; Zoboli and Pillola, 2018), at least two generations of dune deposits are identified. The oldest aeolian deposits were assigned to the Middle Pleistocene (“Funtana Morimonta Fm.”, FMF) and the most recent ones to an undefined Late Pleistocene. The local geological context indicates that the FMF is older than the substage MIS 5e, due to the relationships observed in the Funtanamare shoreline (Gonnesa) (Orrù and Ulzega, 1986). In the Gonnesa Gulf, the Tyrrhenian marine deposit lies on the erosional surface cutting the aeolianites of the FMF. The second aeolian complex (post-Tyrrhenian) crops out in several localities in the Gonnesa area (Orrù and Ulzega, 1986).

2.2.2. The ichnofossil record

To date, only three ichnotaxa related to large mammals have been reported in the Middle-Late Pleistocene record of Sardinia: *Bifidipes* isp., *Canipeda* isp. and *Proboscipeda panfamilia* McNeil, Hills, Tolman, and Kooyman, 2007. The ichnofossils are represented by short trackways and some isolated footprints impressed in aeolian and/or coastal sandy deposits.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Proboscipeda* Panin and Avram, 1962

Type Ichnospecies *Proboscipeda enigmatica* Panin and Avram, 1962

Proboscipeda panfamilia McNeil, Hills, Tolman, and Kooyman, 2007

Figs. 4e, 5 c-f

The footprints assigned to this ichnotaxon have been reported only in the site of Funtana Morimonta (Gonnesa), in Middle Pleistocene aeolian well-cemented coarse sandstone (Pillola and Zoboli, 2017). The recovered specimens are represented by isolated manus-pes couples preserved as convex hyporeliefs or concave epireliefs. Furthermore, proboscidean tracks are clearly visible in transverse sections in the field. The nature of the sediment did not allow the impression and preservation of detailed morphological features and the free digit impressions are not preserved in all specimens.

MPC - B (Fig. 5c) is an incomplete manus-pes set preserved as a concave epirelief with the pes impression overstepping the manus impression. The estimated size of the restored footprints is approximately 20.0 cm x 25.0 cm. A convex volume of deformed sediment by a manus-pes couple is clearly visible in MPC - A (Fig. 5d), even in this case, the pes imprint partially oversteps the posterior part of the manus imprint. The specimens MDLCA 23636 and MDLCA 23637 (Fig. 5 e-f) are represented by a convex hyporelief of an isolated manus-pes couple (Fig. 5e), and its corresponding incomplete concave epirelief (Fig. 5f). The estimated size of the manus imprint is 20.0 cm and 25.0 cm in length and width, respectively. The incomplete epirelief (Fig. 5f2) shows the underlying laminae deformation (undertrack).

Given the size, ovoidal shape, age and occurrence of mammoth body fossils in the same aeolian deposits, the footprints of Gonnesa can be likely attributed to the dwarf Sardinian mammoth *Mammuthus lamarmorai* (Major, 1883), to date the only proboscidean reported in the Pleistocene fossil record of Sardinia. The holotype of this taxon was indeed found closely to the footprints site at the end of the 19th century (Acconci, 1881; Comaschi Caria, 1965; Palombo et al., 2012b; Zoboli et al., 2018). The Sardinian mammoth probably reached 140-160 cm in height and 500 kg in weight. The antero-posterior and the mesial diameters of the manus and pes, based on the skeletal reconstruction of the holotype, are 17.0 cm x 21.0 cm (manus) and 20.0 cm x 17.0 cm (pes), respectively. Surprisingly, the correspondence between the size of



Fig. 4 - Footprints of large mammals from the Middle-Late Pleistocene of Sardinia. a-b) megacerine deer footprints from Pistis (photo by Mr. G. Marras); c) megacerine trackways on pebbly coarse sandstones, Late Pleistocene of Porto Paglia (modified from Fanelli et al., 2007); d) cross section showing megacerine deer footprints rather deep undertraces and curved laminae (Middle Pleistocene of Funtana Morimenta); e) sandstone cross-section showing a pigmy mammoth footprint (Middle Pleistocene of Funtana Morimenta).

the footprints and the bone remains of manus/pes is remarkable, even though the volume of the fleshy portion is unknown and the exact outline of the manus/pes are not well-defined in the tracks (Pillola and Zoboli, 2017).

Ichnogenus *Bifidipes* Demathieu, Ginsburg, Guerin,
and Truc, 1984

Type Ichnospecies *Bifidipes velox* Demathieu,

Ginsburg, Guerin, and Truc, 1984

Bifidipes isp.

Figs. 4 a-d, 5 a-b

Megacerine deer tracks and trackways are present in several localities along the northern and western coasts of Sardinia (Fig. 1a). The ichnofossils have been found on naturally exposed surfaces mainly corresponding to originally stiff or firm sandy carbonate mud, and fine, coarse or pebbly sands having more or less high moisture content. Fanelli et al. (2007) recognized two morphotypes: 1) trackways (two or more consecutive footprints belonging to a single individual) that can be followed for meters (the longest documented consist of about 3-4 m, Fig. 4c); 2) groups of several tracks, sometimes overlapping in various degree, that can be observed within rather restricted trampling areas (about 50 square cm), thus the original direction of movement cannot be detected. Some footprints appear as “simple tracks”, where the tracks of pes and manus are separated and do not overlap. “Compound tracks”, where the tracks of manus and pes overlap or coincide in various degrees, produced a double track; the last type seems to be more frequent (see Fanelli et al., 2007 for further information). Deer tracks have been left in different type of sediments: sandy mud, damp sand and pebbly sand (Fanelli et al., 2007; Zoboli and Pillola, 2018).

Ichnogenus *Canipeda* Panin and Avram, 1962

Type ichnospecies *Canipeda longigriffa* Panin and

Avram, 1962

Canipeda isp.

Fig. 5a

A single footprint (Fig. 5a2) related to a small canid represents to date the only carnivorous ichnofossil in the Pleistocene record of Sardinia. The canid ichnofossil, associated with some deer footprints referable to *Bifidipes* isp. (Fig. 5a1), has been collected in the Porto Paglia area (Fig. 1a). The footprint is preserved as concave epirelief, it is digitigrade and symmetrical with four well-developed toe pads and relative claw marks, and its central pad is not clearly visible.

In Sardinia during the Pleistocene, two dog species belonging to the endemic genus *Cynotherium* are known: *C. sardous* Studiati, 1857 (Middle-Late Pleistocene) and *C. malatestai* Madurell-Malapeira et al., 2015 (?late Early Pleistocene and/or Early Middle Pleistocene). The dog footprint from Porto Paglia is likely referable to *Cynotherium*, and has been assigned to the ichnogenus

Canipeda Panin and Avram, 1962 by Zoboli and Pillola (2018).

2.2.3. Remarks

As regard proboscidean ichnofossils, large footprints and trackways of “normal sized” putative elephants have been described from different localities of Eurasia, Africa and America (e.g. Aramayo and Bianco, 1987; Lucas et al., 2007; McNeil et al., 2007; Neto de Carvalho, 2010; Bibi et al., 2012; Aramayo et al., 2015). *Proboscipeda enigmatica*, the earliest name proposed for deinotheres tracks, was erected to describe ichnofossils from the Miocene of Romania (Panin and Avram, 1962). This ichnotaxon has specific dimensions (14.0 to 17.0 cm in diameter and 42.0 to 52.0 cm in circumference), oval shape (longer than wide) and mostly lacking free digit impressions (Panin and Avram, 1962; McNeil et al., 2007). Abbassi et al. (2017) reported the oldest known proboscidean tracks, assigned to *Proboscipeda enigmatica* and cf. *Proboscipeda* isp., in the Late Eocene of Iran. The footprint-group name *Proboscipeda* is usually used to denote all Cenozoic (from Eocene to the present) large mammals tracks, diagnosing the group as very broad (11.0-62.0 cm in diameter), ovoidal to circular depressions that may show digit impressions, and typically showing overstepping of manus and pes imprints in trackways. *Proboscipeda panfamilia* was proposed by McNeil et al. (2007) to indicate proboscidean tracks from the Pleistocene of Alberta (Canada). These tracks can be distinguished from the smaller *P. enigmatica* by their average large size and more circular shape. *P. panfamilia* impressions range between 11.0 and 62.0 cm in diameter (including juvenile trackmakers) and are characterized by bilateral symmetry and a nearly circular outline. Lucas et al. (2007) described *P. panfamilia* attributed to *Mammuthus columbi* (Falconer, 1857) from the Late Pleistocene of New Mexico. Finally, Neto de Carvalho (2010) reported mammal and bird footprints in the Pleistocene of Portugal and *P. panfamilia*, possibly related with *Elephas antiquus* Falconer and Cautley, 1847. Therefore, *P. panfamilia* was chosen to designate the occurrence of many different sized tracks, representing very young to old mammoths and straight-tusked elephants. Pigmy proboscidean footprints were reported in coastal areas of the SW part of the island of Rhodes, Greece (Milàn et al., 2007). Outside the Mediterranean region, other footprints likely produced by small elephants were described by Matsukawa and Shibata (2015) in the Miocene of Japan and attributed to the pigmy insular species *Stegolophodon pseudolatidens* (Yabe, 1950). Considering shape and size, the Sardinian ichnofossils were assigned to the ichnotaxon *P. panfamilia* by Pillola and Zoboli (2017). Furthermore, the possible trackmaker identified is the pigmy mammoth *Mammuthus lamarmorai* (Major, 1883).

As regard artiodactyls, the megacerine deer *Praemegaceros* is the only large taxon reported in the Middle-Late Pleistocene record of Sardinia. Remains ascribed to this taxon are relatively frequent in aeolian

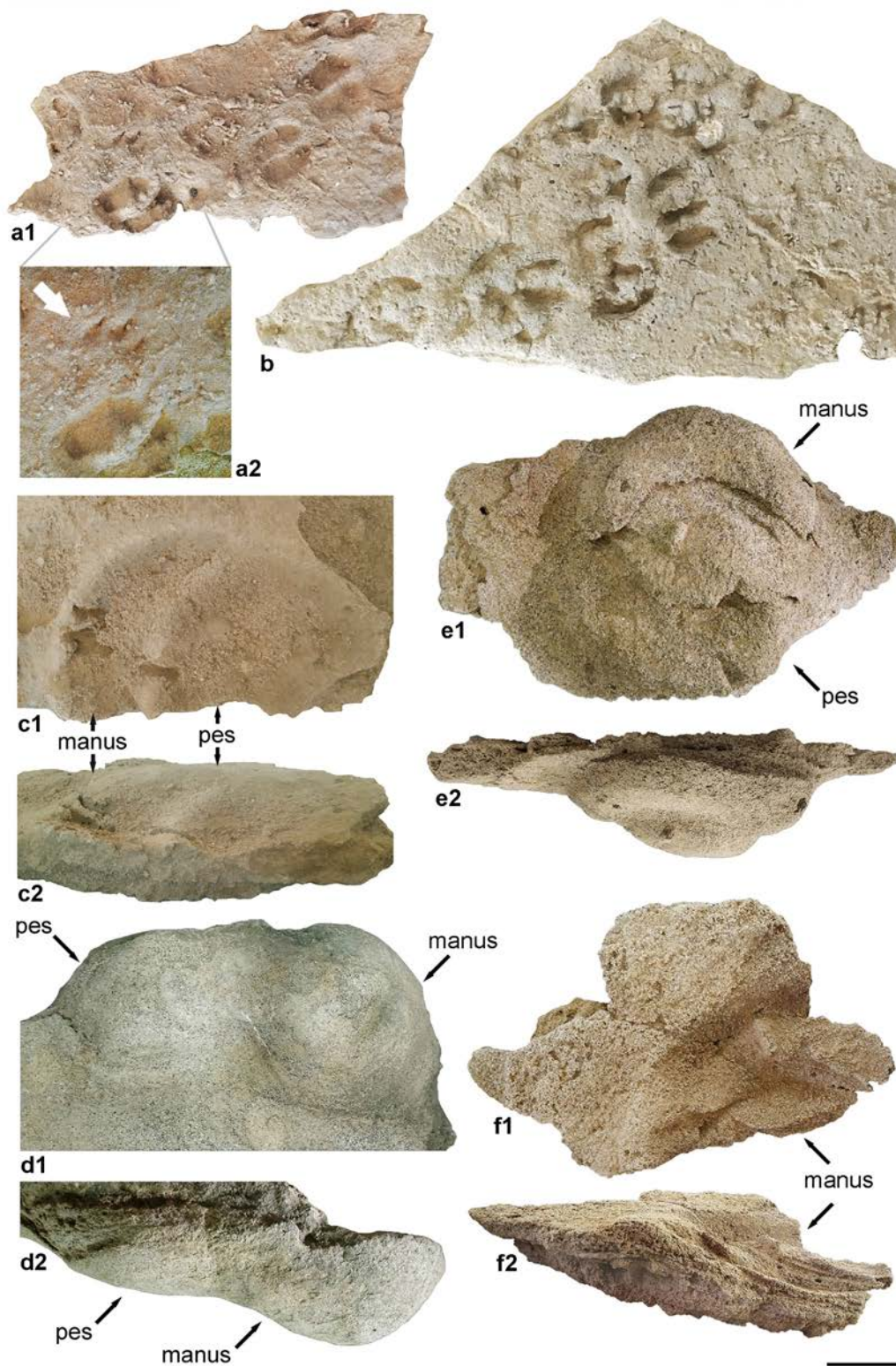


Fig. 5 - Middle-Late Pleistocene vertebrate ichnofossils of Sardinia. a) *Bifidipes* isp. and *Canipeda* isp. (GLP 0179), trampled bedding surface showing deer tracks and a single canid footprint (a1), detail of *Canipeda* isp. (a2), Porto Paglia (Gonnesa); b) *Bifidipes* isp. (GLP 0180), trampled bedding surface showing single and compound tracks impressed on sandy carbonate mud, Porto Paglia (Gonnesa); c) *Proboscipeda panfamilia* (GLP 0177), incomplete epirelief of manus-pes couple in superior (c1) and lateral (c2) views, superimposed deer tracks are visible on the left, Funtana Morimenta (Gonnesa); d) *Proboscipeda panfamilia* (MPC - A), manus-pes hyporelief in inferior (d1) and lateral (d2) views, Funtana Morimenta (Gonnesa); e) *Proboscipeda panfamilia* (MDLCA 23636), manus-pes hyporelief in inferior (e1) and anterior (e2) views, Funtana Morimenta (Gonnesa); f) *Proboscipeda panfamilia* (MDLCA 23637), part of epirelief in superior (f1) and lateral (f2) views, Funtana Morimenta (Gonnesa). GLP and MPC: specimens stored at the Museo dei Paleoambienti Sulcitani - E.A. Martel of Carbonia; MDLCA: specimens stored at the Museo Sardo di Geologia e Paleontologia "D. Lovisato", University of Cagliari. Scale-bar for a1, b-f = 10 cm; scale-bar for a2 = 5 cm.

(s.l.) deposits (Comaschi Caria, 1955a, 1955b); fissure fillings (Studiati, 1857; Abbazzi et al., 2004; Van der Made and Palombo, 2006; Zoboli and Pillola, 2016, 2017; Zoboli et al., 2019) and cave deposits (Caloi and Malatesta, 1974; Melis et al., 2016). Currently, two species are reported from Sardinia: *Praemegaceros cazioti* (Depéret, 1897) and *Praemegaceros sardus* (Van der Made and Palombo, 2006). This latter taxon is considered the ancestor of *P. cazioti* and its size is about 25-40% larger than *P. cazioti* (Van der Made and Palombo, 2006). Moreover, the fossil remains of a large deer from Su Fossu de Cannas Cave (Sadali) indicate the most primitive megacerine deer found in Sardinia and the first representative of the Sardinian endemic lineage (Melis et al., 2016).

During the Middle-Late Pleistocene, the endemic megacerine deer were present in coastal areas, such as beaches and dunes, where probably they were attracted by salt crusts, as it occurs nowadays. For this reason, herds of deer and single males were usual frequenters of these places, which are particularly suitable for track preservation. The most suitable environment is represented by tidal and flood plains, lagoons periodically subject to water level oscillations and even complete desiccation, and distal portions of washover fans, where moist, coherent, fine-grained sediments are present (Fanelli et al., 2007). As far as the megacerine footprints are concerned, they were impressed, as in sub-modern environments, on various substrates, ranging from moist coarse to fine sands and rather plastic sandy carbonate mud. The depositional environment could be represented by stagnation areas, covered by a fine water film, periodically subjected to desiccation. According to Fanelli et al. (2007) the megacerine tracks have been recognized on bed surfaces, from distal fan depositional environments or lagoonal edge (low-energy shallow waters) and backshore deposits. The presence of defined tracks and pressure pads on these bedding surfaces suggest a moist substrate, not wet, and

periodically dried. The comparison between the trackway parameters on different substrates left by modern cervids (e.g. *Cervus elaphus* and *Dama dama*) are similar to those produced by the Sardinian insular megacerine; in particular, the parameters are very close to those of the modern *Cervus elaphus* (Fanelli et al., 2007).

The ichnological and sedimentological data indicate a rather accurate palaeoenvironmental scenario for the western Sardinia during the Middle-Late Pleistocene. Most likely, herds of megacerine deer and groups of pigmy mammoths wandered in search of trophic resources in large expanses of dunes blown by the mistral and dotted with ephemeral marshes or coastal lagoons (Fig. 6).

3. QUATERNARY VERTEBRATE ICHNOFOSSILS RECORD OF THE ITALIAN PENINSULA: AN OVERVIEW

In spite of the remarkable mammalian fossil record, only a few tracks and trackways have been recorded in the continental Italy Pleistocene deposits. Few large footprints, possibly left by *Mammuthus meridionalis*, have been detected, for instance, in the aeolian-reworked alluvial sandsheet deposits of Upper Valdarno (“sabbie del Palazzetto”, unit VRCb, Chianti; pre-Olduvai Early Pleistocene) (Ghinassi et al., 2013), whereas traces left by cave bear, commonly identified as *Ursichnus europaeus* Diedrich, 2011 ichnospecies have been reported from few late glacial cave, such as “Grotta del Fiume” (Gola di Frasassi, Ancona, Marche) (Bocchini and Coltorti, 1978), and the well-known “Sala dei Misteri” (Bàsura Cave, Toirano, Liguria) (Citton et al., 2017).

In the Holocene, a number of tracks and trackways, mainly made by domesticated animals, have been mainly reported from archaeological sites, particularly from volcanic ash deposits of protohistorical and historical sites (Kim et al., 2008). More specifically, footprints of



Fig. 6 - Palaeoenvironmental reconstruction of a dune landscape of Sardinia during the Middle-Late Pleistocene and vertebrate community interpreted on the basis of the ichnofossil data, from left to right: *Mammuthus lamarmorai*, *Cynotherium* sp. and *Praemegaceros* sp. (from Zoboli and Pillola, 2018).

mammals have been found on the uppermost levels of the Pomici di Avellino eruption (Somma-Vesuvius Volcano, 3945 ± 10 BP, 1995 ± 10 cal BC) (Sevink et al., 2011; Di Lorenzo et al., 2013; Di Vito et al., 2019), and at Croce del Papa (Nola) (Di Vito et al., 2009, 2018, 2019; Laforgia et al., 2009) and at the Bronze Age village of Afragola-Badagnano (Vesuvius Volcano) (Di Vito et al., 2009, 2018, 2019; Laforgia et al., 2013). Several mammal footprints have also been recently found at the Neolithic settlements of Casetta Mistici and Tor Vergata (Rome) on the surface of lahar sediments, arising from the crater of the Albano Lake (Cerilli et al., in press).

Particularly rare, in Italy, are Middle Pleistocene vertebrate tracks. Fossil record of mammal tracks are thus far only recorded at the “Devil’s Trails” Foresta palaeontological site (Foresta Village, north-eastern slope of the Roccamonfina Volcano, Tora e Picilli municipality, Fig. 1b), well-known for its exceptional hominin footprints (see Avanzini et al., 2020 and references therein).

The mammal tracks and trackways identified, thus far at the ichnosite are few, but deserve attention because provide some clues about the animals that shared the same territory with the Early Palaeolithic humans, at the time they walked on the still unconsolidated Roccamonfina ignimbrite deposit (a unit of the Brown Leucitic Tuff) around 350 ka ago (for further information about mammalian fauna and human remains see, among others, Biddittu et al., 1979, 2020; Biddittu and Segre, 2009; Manzi et al., 2011; Palombo, 2014, 2018a, 2018b; Peretto et al., 2014, 2016; Manzi, 2016; Pereira et al., 2016, 2018; Zanolli et al., 2018 and references in those papers).

3.1. MAMMAL TRACKS AND TRACKWAYS FROM THE MIDDLE PLEISTOCENE FORESTA ICHNOSITE (ROCCAMONFINA VOLCANO, CENTRAL ITALY)

3.1.1. Geological context

The Roccamonfina Volcano, located in the NE-trending Garigliano graben (Fig. 1b), is one among the various volcanos and volcanic districts of the Roman magmatic province, which extends from about the western side of the Central Apennines to the Tyrrhenian margin, between the Ancona-Anzio/Olevano-Antrodoco and the Ortona-Roccamonfina tectonic lines (Peccerillo, 2017).

The Roccamonfina stratovolcano is characterized by two stages of volcanic activity separated by volcano-tectonic caldera collapses, which occurred at about 400 ka. The first phase was dominated by leucite-bearing lava flows inter-bedded to minor ashfall and mud-flow deposits, and lasted from about 630 and 400 ka. During the second plinian paroxysmal volcanic phase, lasting from about 385 and 230 ka, the deposition of the pyroclastic Brown Leucitic Tuff and White Trachytic Tuffs flow units took place. The central shoshonitic domes formed during the latest stage of activity at about 150 ka (De Rita et al., 1998; Rouchon et al., 2008; Santello, 2010 and references

therein).

The stratigraphy of the BLT reflects the evolution of pyroclastic currents originated by collapses of eruptive columns. Eight pyroclastic units (LS1 to LS8), bounded by unconformity surfaces, have been detected. The human and mammal footprints were impressed very shortly after the emplacement of pyroclastic flows, on the top of the cooling and still unconsolidated surface of the distal region of the ignimbritic flow corresponding to the LS7 pyroclastic unit. The lithification process that affected the flow deposit as the result of a zeolitization process permitted the tracks to be preserved (Santello, 2010). A couple of mammal footprints were impressed on the surface of a discontinuity layer interbedded between LS7 and LS8, which ranges from 2 to 11 cm in thickness.

The recent radiometric $^{40}\text{Ar}/^{39}\text{Ar}$ date obtained for both LS7 and on LS8 implies a very short time gap between the two explosive events and indicates that hominins and mammals were present in the area and left their traces by the end of MIS 10, in a time close to the Climatic Termination IV (Santello, 2010; Panarello et al., 2017a, 2020 and references therein). For further information see Avanzini et al. (2020).

3.1.2. The ichnofossil record

The detection and identification of vertebrate footprints on the ignimbrite palaeosurface is challenging due to the characteristics of the pyroclastic flow (e.g. coarse granulometry, presence of centimeter-sized clasts, pumice concentration zones), which may hamper the preservation of anatomical details, together with the alteration undergone in the top of the volcanoclastic deposit during its prolonged exposure to weathering agents. The latter might have determined, for instance, the obliteration of shallow footprints impressed by small-sized animals and/or by animals walking on the ignimbrite at the time that the zeolitization processes had already made quite firm its surface.

Two short mammal trackways, and some isolated footprints have been identified at Foresta ichnosite. The limited record prevents, for the most part, a firm-specific attribution and makes problematic to identify the trackmaker. To date, four ichnotaxa have been identified (ichnospecies *Proboscipeda panfamilia*, McNeil, Hills, Tolman, and Kooyman, 2007; ichnogenus *Ursichnus* Diedrich, 2011 and *Hippipeda* Vyalov, 1965, emended Vyalov, 1966; ichnogenus *Pecoripeda* Vyalov, 1966).

SYSTEMATIC ICHNOLOGY

Ichnogenus *Proboscipeda* Panin and Avram, 1962
Type Ichnospecies *Proboscipeda enigmatica* Panin and Avram, 1962

Proboscipeda panfamilia McNeil, Hills, Tolman, and Kooyman, 2007

Fig. 7 a-c

The footprints assigned to *Proboscipeda panfamilia*, preliminarily described by Palombo et al. (2018), consists

of some isolated impressions (manus and pes), preserved as concave epireliefs, organized in a quite narrow, short trackway left by a young elephant that walked along the edge of the slope near the ancient pathway along which also human trackmakers walked (Panarello et al., 2017a). Few tracks are well preserved and show some anatomical details (i.e. toe/nail impressions), whereas others potential footprints cannot be firmly validated because located in an area that has undergone strong anthropic alteration and currently is subject to degradation, due to the action of surface runoff water (Fig. 7a). The footprints, nearly rounded to oval in shape, are preserved as convex hyporeliefs, bordered by more or less inflated and prominent pressure pads.

The best preserved footprints (M1-L, M2-R) (Fig. 7b) were left by the anterior feet, as the oval shape, with a width exceeding the length, clearly indicates. In both, the imprinting deepest zone corresponds to the front part, which is opposite of dip, following the typical elephant foot rotation during the event foot on - foot off. The sharp frontal edges of the toe impressions, particularly evident in M1-L, indicate the presence of nails, suggesting the tracks were left by a young individual (Fig. 7b). The nails, indeed, are usually worn down in adult elephants and hardly ever leave clear impressions. M2-R footprint presents the typical lateral expansion that is formed by dragging during the lifting phase of the foot at the end of the step.

The estimated size of the footprints M1-L and M2-R (length x width = 248.05x277.17 mm and 329.43x334.82 mm respectively) support the hypothesis that it is a young elephant trackmaker. Based on the results of the analysis carried out by Palombo et al. (2018), the Foresta footprints should have been left by an elephant aged 4-9 years, if female, or 5-8 years, if male, with a shoulder height of approximately 1.9 m and a weight between 2350 kg (calculated using the circumference of the front foot derived from the size of the footprint M1-L as a variable) and 2600 kg (calculated using shoulder height as a variable) (see Palombo and Giovinazzo, 2005).

The morphology and proportionally large size of the footprints allow to identify them as belonging to the ichnospecies *Proboscipeda panfamilia*, to which are ascribed, among others, the traces of the species of the tribes Loxodontini (genus *Loxodonta*) and Elephantini (genera *Elephas*, *Palaeloxodon*, and *Mammuthus*) (Shoshani and Tassy, 2005). It is, however, difficult to identify the species to which the elephant that left these footprints could belong. The analysis of the footprints left by current elephants on different substrates has shown, in fact, how, in the footprints left by the same individual, the traces of the nails/fingerprints could be absent or present depending on the type of substrate and how this character cannot be considered as diagnostic (Pasenko, 2017).

Some support for a hypothetical identification of the trackmaker of the Foresta footprints could be given by the fact that, during the Middle Pleistocene, *P. antiquus* was widely spread in the Italian Peninsula, particularly

in central Italy where, in some local faunas, it was one of the dominant species (see, for example, La Polledrara di Cecanibbio, Anzidei et al., 2004, 2012; Pereira et al., 2017), whereas the presence of the steppe mammoth, *Mammuthus trogontherii*, is documented in very few places (Palombo and Ferretti, 2005). To note that in southern Lazio and southern Italy, remains of *P. antiquus* are reported, since the last century, in most of the sites where the presence of *H. heidelbergensis*-like hominins is testified by the discovery of Lower Palaeolithic artifacts (De Lorenzo and D'Erasmus, 1932; Biddittu and Segre, 2009 and references therein), as well as by some humans remains, such as the skull found at Ceprano, a site close in age and geographical location to the Foresta ichnosite (Manzi et al., 2010, 2011; Biddittu et al., 2020). The hypothesis that the Foresta elephant was a young *P. antiquus* is, therefore, the most plausible, though not objectively demonstrable.

Finally, it is worth noting that footprints ascribed to *P. panfamilia* and attributed to *P. antiquus* have been reported in the Iberian Peninsula (Portugal, Neto de Carvalho, 2010, 2011; Neto de Carvalho et al., 2016; Spain, Valle Manzanares, Panera et al., 2014; Gibraltar, Muñiz et al., 2019), whereas in the islands of the eastern Mediterranean (Rhodes and Cyprus), the traces were left by endemic elephants variously reduced in size (Milán et al., 2007, 2015).

Assuming as true the hypothesis that the Foresta elephant footprints could actually belong to *P. antiquus*, they would be the only *Palaeloxodon* footprints reported from Italy and the oldest ones of straight-tusked elephants known so far in Europe.

Ichnogenus *Ursichnus* Diedrich, 2011

Type ichnospecies *Ursichnus europaeus* Diedrich, 2011

Ursichnus isp.

Fig. 7f

A couple of footprints have been detected on a fine to coarse-grained, locally muddy horizon laying at the top of LS7 layer, and covered in apparent stratigraphical continuity, by the thin layer interposed between the surface of the LS7 unit and the base of the LS8 unit. Ongoing volcanological research will enable to better specify the characteristic and the chronostratigraphical position of this horizon.

The footprints show some similarities with those of the representatives of the genus *Ursus*, for whom the new ichnogenus and ichnospecies *Ursichnus europaeus* were proposed by Diedrich (2011). As highlighted by the German author, bear manus and pes differ in shape (e.g. the heel is small and ovoid in manus, large and triangular in pes) and proportions (with manus/pes length ratio of about 1:1.25), the claw impressions may be absent, mainly depending of the substratum, as well as the manus track does, depending on the quadrupedal or bipedal walking of the individual (Diedrich, 2011).

The Foresta footprints were impressed on a muddy



Fig. 7 - Foresta "Devil's Trails" ichnosite, mammals fossil footprints. a-c) Proboscipeda panfamilia, eastern overview of the trackways with the footprints left by a young straight-tusked elephant (*Palaeoloxodon antiquus*), the box shows the footprints analysed so far (a), oblique photo of the left hand impression (ML-1) in which the traces left by the nails are visible (b) oblique photo of the right hand impression (MR-1) in which the drag-structure is visible (c), scale-bar = 10 cm; d) *Hippipeda* isp., southern zenithal 3D generated image of the trackway of footprints left by a medium-sized *Equus* sp., scale-bar = 60 cm; e) artiodactyl tracks, northern zenithal image of footprints left by a medium-sized artiodactyl, scale-bar = 10 cm; f) *Ursichnus* isp., footprint likely left by a medium sized bear (*Ursus* sp.), scale-bar = 10 cm.

surface in a period immediately following the time that hominins and elephants crossed the palaeo-pathway. Mud cracks are present on both the footprints and the level surfaces accounting for the contemporaneity of traces with the level they were impressed on, and perhaps for limited water content of the muddy sediment. The best-preserved track, a sub-oval, roughly kidney-shaped large depression, would correspond to the manus. Five small oval depressions along its convex edge, i.e. in front of the pad, may correspond to digit impressions. Some pits in front of the 'digit impression' would correspond to claw marks, considering that the claw marks of bear sometimes may be slightly marked if the footprint are left on soft surfaces. The preliminary analysis does not enable us to detect all the diagnostic traits and anatomical details required for indisputably confirming the footprint identification, which needs to be supported by further study.

Ichnogenus *Hippipeda* Vyalov, 1965; emended Vyalov, 1966, p. 137
Hippipeda isp.
 Fig. 7d

To the genus *Hippipeda* can be ascribed at least three well-defined footprints and some other quite badly preserved cavities, aligned in a short trackway, running obliquely along the ignimbrite slope and crossing the hominin Trackway B. The footprints, monodactyl, mesaxonic (as typical of perissodactyls, in which the weight falls on the central toe), subcircular, with the front part markedly convex that tends to expand laterally where the margins have a subparallel trend, are very similar to each other in shape and size and it is difficult, for the moment, to distinguish the manus from pes impressions.

The hemi-ellipsoidal shape, the remarkably deep anterior part, the sometimes conceivable presence of the V shaped frog at the rear margin of the footprint (though barely discernible between the two posterior wall bars), indicate that the footprints have been impressed by a representative of the genus *Equus*.

The footprints have not yet been analyzed in depth. Therefore, the presence of anatomical details typical of this ichnogenus, such as the deepest curvilinear trace left antero-laterally by the wall of the hoof, the moderately connected central part corresponding to the sole, and the rear cuneiform inlet, with apex facing the tip, placed between the bars of the wall and housing the slicer (or fork) cannot confidently be confirmed.

Due to the very preliminary stage of the study, the identification has to be regarded as indicative, although highly probable.

Ichnogenus *Pecoripeda* Vyalov, 1966
 ? Ichnosubgenus *Cervipeda*, Vyalov, 1966
 Fig. 7e

The best-preserved mammal footprints among those

identified so far in the Foresta ichnosite, are a couple of didactylous impressions belonging to a medium-small sized artiodactyl.

Various ichnogenic names have been proposed for artiodactyls (even toed) didactylous footprints, such as *Pecoripeda* Vyalov, 1966, *Entelodontipus* Casanovas and Santafé, 1982, and *Bifidipes* Demathieu et al., 1984.

Vyalov (1966) created the ichnogenic names *Pecoripeda* and *Suipeda* respectively for ruminant and non-ruminant footprints and the ichnosubgenus *Cervipeda* for those of deer representatives. Successively, Demathieu et al. (1984) created the ichnogenic name *Bifidipes*, including both cervid and bovid footprints. Although the name *Pecoripeda* has the priority, other name, particularly *Bifidipes*, have been largely adopted in ichnotaxonomy. To note, moreover, that the classification proposed by Vyalov (1966), though conceptually sound because based on extant animal tracks, is sometimes difficult to apply to the ichnofossil record. Discussion of the validity of the artiodactyl ichnogenes is beyond the scope of this research. Consequently, taking also in account that we used the ichnogenic name *Bifidipes* for the Capu Mannu footprints (see above the section 2.1.2. for a discussion), we prefer to adopt an open taxonomical identification for the Foresta artiodactyl footprints.

The Foresta didactylous impressions, located in the sub-planar area of the ancient pathway with a direction about perpendicular to the latter, indicate that the trackmaker moved towards the slope. They belong to a middle-sized ruminant that left the four large impressions of the left and right medial digit III and lateral digit IV hoof, and, on the back, those, smaller, of the dewclaws, the vestigial hooves for digits II and V (Fig. 7e). The large concave hyporeliefs of the two hooves, each other specularly arranged, show the typical elongated, sub-cuneiform shape with a convex, parabolic external and slightly concave internal contour, angled distal and wide caudal part. The dewclaw impressions are considerably smaller, nearly fused each other, and sub-quadrangular in shape.

The identification of the species to which the trackmaker belongs is challenging due to the similarity in the basic morphology, which characterizes the footprints left by ruminant artiodactyls of medium size, and the morphological and dimensional variability of footprints left by middle-sized cervids and bovids depending the sex and the age of the trackmaker, or even the traces left by a single individual according to the gait and the substrate. The difficulty in identification increase when only few footprints are preserved, as it is the case of Foresta. Based on the presence of small dewclaw impressions, the dimensions, proportions and shape of the impressions left by the digit II and V hooves, we may hypothesize the trackmaker was a roe deer, though such hypothesis has to be considered with a great caution (see discussion in Panarello et al., 2017a).

3.1.3. Remarks

Although not numerous and in some aspects difficult

to decipher, the Foresta mammalian footprints constitute a valuable component in the context of the Italian palaeoichnology because they are the only footprints known to date in the Italian peninsular Middle Pleistocene and should also be regarded as an unicum due to the nature and steepness of the substrate they are impressed on. Moreover, in the attempt to hypothesize what the environment of Roccamonfina could have been at the time that hominins walked leaving the well-known “Devil’s Trails” along the ancient Foresta pathway, the mammal fauna ichnological record would provide some information when data on flora and fauna are missing.

We are aware, however, that the pieces of information coming from the preliminary study of Foresta mammal footprints are not enough for inferring the basic characteristics of the palaeoenvironment, due to the uncertain identification of trackmaker species and their low number. The alleged presence of the European roe deer *Capreolus capreolus*, if confirmed, and of a bear, would imply a wooded environment, because forests are the preferred habitat of all the species recorded in Europe in the period corresponding to the end of MIS 11 and MIS 10 (*Ursus deningeri*, *Ursus arctos*, *Ursus thibetanus*). If, as probable, the footprints of the elephant belong to *P. antiquus*, the most congenial environment would be a savanna-like, a mixed woodland-grassland ecosystem, while if the trackmaker was a young *M. trogontherii*, the environment would be a steppe grassland. The presence of *Equus* footprints, whatever the species should be, indicates the presence of grasslands and open spaces with herbaceous vegetation. The possible presence at the Foresta ichnosite of mammals preferentially inhabiting both forest and open environments and the fact that hominins presence at the site is attested by the end of a glacial phase (MIS 10), the hypothesis of the persistence, in the Roccamonfina area, of forest areas, possibly mainly located in the valleys, and open spaces with herbaceous vegetation seems to be the most probable. New data are, however, necessary to confirm or reject this hypothesis as well as for a better understanding of the behaviour, in terms of resource exploitation and settlement choices, of human groups during a glacial cycle and in response to the peculiar stimuli induced by life in a volcanic environment during a cold climatic phase. During the same cold period, hominin groups still inhabited the nearby site of Guado San Nicola (Molise), where lithic artifacts document their prolonged presence during MIS 11-MIS 10 (between 400±9 ka and 345±9 ka) (Pereira et al., 2016; Peretto et al., 2016 and references therein). The mammal remains found at this site belong to species inhabiting a diversity of environments, although wooden grassland and open landscape seem dominating, but mammals preferring closed environments are also present. The site was located on the banks of a river, and, according to Orain et al. (2013), the local humidity could have facilitated the persistence of localized wooded areas. The resulting diversity of exploitable resources, the presence of water surrounded by vegetation, and in turn the presence of a

diversified fauna were undoubtedly attractive aspects for hunter-gatherer groups. This may be the reason of the long-lasting presence of hominins at Guado San Nicola, as well as the attendance of the Roccamonfina territory.

The ongoing studies and research will provide fresh clues for a better understanding the Foresta palaeoenvironmental context and the kind and amount of resources available for the hominin groups inhabiting this territory around 350,000 years ago.

4. CONCLUSIVE REMARKS

The Pleistocene vertebrate ichnological record of Italy is represented only by tracks and trackways left by large mammals (excluding the hominid ichnofossils) reported from various localities of Sardinia, Liguria, Tuscany, Marche and Campania ranging in age from the late Early to the last glacial. A number of Holocene tracks and trackways, mainly made by domesticated animals, have been reported particularly from volcanic ash deposits of protohistorical and historical sites.

In this research, we provide a critical inventory of the Pleistocene mammalian tracks and trackways thus far reported from western Sardinia and from the well-known site of Foresta “Devil’s Trails” (Campania). Specifically, the vertebrate ichnofossils herein discussed originate from several Sardinian localities, and from the Middle Pleistocene ichnosite of Foresta (Campania).

The vertebrate ichnofossils of Sardinia were found in aeolian deposits (s.l.) mainly localized along the northern and western coasts of the island. Four ichnotaxa are reported in the Sardinian Early-Late Pleistocene localities: *Bifidipes* aff. *B. aeolis* in the Early Pleistocene dunal system of Capo Mannu (central-western Sardinia), and *Proboscipeda panfamilia* McNeil, Hills, Tolman, and Kooyman, 2007, *Bifidipes* isp. and *Canipeda* isp. in various Middle-Late Pleistocene sites.

The Middle-Late Pleistocene ichnological and sedimentological data provide some hints to infer the Sardinian palaeoenvironmental scenario at that time. Along the coasts, where northwestern dominant winds accumulated extensive dunal deposits especially during arid periods, herds of megacerine deer and groups of pigmy mammoths wandered across the wide dune landscape dotted with ephemeral marshes, intradune ponds, and coastal lagoons in search of trophic resources as modern Sardinian deer do still nowadays.

The Middle Pleistocene ichnological record of Foresta “Devil’s Trails” consists of tracks and trackways attributable to four large mammal ichnotaxa: *Proboscipeda panfamilia*, McNeil, Hills, Tolman, and Kooyman, 2007, *Ursichnus* isp., *Hippipeda* isp., and the ichnogenus *Pecoripeda* (? ichnosubgenus *Cervipeda*). The Middle Pleistocene mammal footprints reported at the site constitute a valuable component in the context of the Italian palaeoichnology because they are the only known to date for this slice of time. The small Foresta ichnofossil record does provide enough information for any palaeoenvironmental

reconstruction. The possible presence at the Foresta ichnosite of mammals preferentially inhabiting both forest and open spaces with herbaceous vegetation by the end of a glacial phase (MIS 10), may suggest, however, that in the Roccamonfina area some forest persisted, possibly mainly located in the valleys.

ACKNOWLEDGEMENTS - GLP was supported by the Università di Cagliari CAR Project, "Paleobiodiversità: strumento di base in biostratigrafia, in paleoecologia e nella valorizzazione dei beni culturali Geo-Paleontologici". DZ was supported by grants P.O.R. Sardegna F.S.E. 2014-2020 - Asse III "Istruzione e Formazione, Obiettivo Tematico: 10, Obiettivo Specifico: 10.5, Azione dell'accordo di Partenariato: 10.5.12 "Avviso di chiamata per il finanziamento di Progetti di ricerca - Anno 2017". We would like to thank Carlos Neto De Carvalho and the anonymous reviewer for their comments that improved the quality of the manuscript.

REFERENCES

- Abbassi N., Alinasiri S., Lucas S.G., 2017. New localities of Late Eocene vertebrate footprints from the Tarom Mountains, Northwestern Iran. *Historical Biology* 29, 987-1006.
- Abbazzi L., Angelone C., Arca M., Barione G., Bedetti C., Delfino M., Kotsakis T., Marcolini F., Palombo M.R., Pavia M., Piras P., Rook L., Torre D., Tuveri C., Valli A.M.F., Wilkens B., 2004. Plio-Pleistocene fossil vertebrates of Monte Tuttavista (Orosei, E. Sardinia, Italy), An overview. *Rivista Italiana di Paleontologia e Stratigrafia* 110, 603-628.
- Abbazzi L., Carboni S., Delfino M., Gallai G., Lecca L., Rook L., 2008. Fossil vertebrates (Mammalia and Reptilia) from Capo Mannu formation (Late Pliocene, Sardinia, Italy), with description of a new *Testudo* (Chelonii, Testudinidae) species. *Rivista Italiana di Paleontologia e Stratigrafia* 114, 119-132.
- Acconci L., 1881. Sopra alcune ossa fossili di Elefante rinvenute nel Quaternario della zona di Morimonta in Sardegna. *Processi Verbali Atti Società Toscana di Scienze Naturali* 2, 266-267.
- Andreucci S., Clemmensen L.B., Murray A.S., Pascucci V., 2010. Middle to late Pleistocene coastal deposits of Alghero, northwest Sardinia (Italy): Chronology and evolution. *Quaternary International* 222, 3-16.
- Andreucci S., Pascucci V., Clemmensen L.B., 2006. Upper Pleistocene coastal deposits of West Sardinia: a record of sea-level and climatic change. *GeoActa* 5, 79-96.
- Angelone C., Kotsakis T., 2001. *Rhagapodemus azzarolii* n. sp. (Muridae, Rodentia) from the Pliocene of Mandriola (Western Sardinia-Italy). *Bollettino della Società Paleontologica Italiana* 40, 127-132.
- Anzidei A.P., Arnoldus A., Palombo M.R., Argenti P., Caloi L., Marcolini F., Lemorini C., Mussi M., 2004. La Polledrara di Cecanibbio, faune, industrie, milieu. In: Baquedano E., Rubio S. (Eds), Homenaje a Emiliano Aguirre. Museo Arqueológico Regional, Madrid Zona Arqueológica 4, 20-29.
- Anzidei A.P., Bulgarelli G.M., Catalano P., Cerilli E., Gallotti R., Lemorini C., Milli S., Palombo M.R., Pantano W., Santucci E., 2012. Ongoing research at the late Middle Pleistocene site of La Polledrara di Cecanibbio (central Italy), with emphasis on human-elephant relationships. *Quaternary International* 255, 171-187.
- Aramayo S.A., Bianco T.M., 1987. Hallazgo de una icnofauna continental (Pleistocene tardio) en la localidad de Pehuen-Co (Partido de Coronel Rosales) provincia de Buenos Aires, Argentina. Parte I: Edentata, Litopterna, Proboscidea. Parte II: Carnivora, Artiodactyla y Aves. IV Congreso Latinoamericano de Paleontología. *Bolivia Actas* 1, 516-547.
- Aramayo S.A., Manera T., Bastianelli N.V., Melchor R.N., 2015. Pehuen Co: Updated taxonomic review of a late Pleistocene ichnological site in Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 439, 144-165.
- Avanzini M., Citton P., Mietto P., Panarello A., Raia P., Romano M., Salvador I., 2020. Human footprints from Italy: the state of the art. *Journal of Mediterranean Earth Sciences* 12, in this volume, doi: 10.3304/JMES.2019.003.
- Bibi F., Kraatz B., Craig N., Beech M., Schuster M., Hill A., 2012. Early evidence for complex social structure in Proboscidea from a late Miocene trackway site in the United Arab Emirates. *Biology Letters* 8, 670-673.
- Biddittu I., Segre A.G., 2009. Pléistocène moyen et inférieur dans le Latium (Italie centrale). *L'Anthropologie* 113, 59-65.
- Biddittu I., Cassoli P.F., Radicati di Brozolo F., Segre A.G., Segre Naldini E., Villa I., 1979. Anagni, a K-Ar dated Lower and Middle Pleistocene Site, Central Italy: Preliminary Report. *Quaternaria Nova* 21, 53-71.
- Biddittu I., Moncel M-H., Milli S., Bellucci L., Ruffo M., Saracino B., Manzi G., 2020. Stratigraphy, sedimentology, and archaeology of Middle Pleistocene localities near Ceprano, Campogrande area, Italy. *Quaternary Research* 93, 155-171.
- Bocchini A., Coltorti M., 1978. Unghiate ed impronte di *Ursus spelaeus* nella Grotta del Fiume nella Gola di Frasassi (Ancona). *Rassegna Speleologia Italiana Memoria* 12, 138-141.
- Bover P., Fornós J.J., 2005. Carpal bones, carpal fusions and footprints of *Myotragus*: clues for locomotion and behavior. *Monografies de la Societat d'Història Natural de les Balears* 12, 59-72.
- Bruijn de H.E., Rümke C.G., 1974. On a peculiar mammalian association from the Miocene of Oschiri (Sardinia). *Proceedings Koninklijke Nederlandse Akademie Van Wetenschappen B* 77, 44-79.
- Caloi L., Malatesta A., 1974. Il cervo pleistocenico di Sardegna. *Memorie dell'Istituto Italiano di Paleontologia Umana* 3, 1-246.
- Carboni A., Lecca L., 1985. Osservazioni sul Pleistocene mediosuperiore della penisola del Sinis (Sardegna occidentale). *Bollettino della Società Geologica Italiana* 104, 459-477.
- Carboni S., Lecca L., 1995. Le Pliocène de Capo Mannu (Sardaigne occidentale): transition marin littoral-continental dunaire. *Comptes rendus de l'Académie des Sciences* 320, 1203-1210.
- Casnovas-Cladellas M.L., Santafe-Llopis J.V., 1982. Icnofauna

- oligocena de Agramunt (Lérida, España). *Acta Geologica Hispánica* 17, 113-119.
- Catto N., 2010. Comment on Commentary Geomorphology, stratigraphy and facies analysis of some Late Pleistocene and Holocene key deposits along the coast of Sardinia (Italy), and Geochronology for some key sites along the coast of Sardinia (Italy): a note from the Editor-in-Chief. *Quaternary International* 222, 46-47.
- Cerilli E., Celant A., Giordano G., Carboni G., in press. 1.2 - Cassetta Mistici e Tor Vergata-San Gaudenzio (Roma): impronte di animali ed umane su una superficie di lahar, In: Anzidei A.P., Carboni G. (Eds.), Roma Prima del Mito.
- Citton P., Romano M., Salvador I., Avanzini M., 2017. Reviewing the upper Pleistocene human footprints from the 'Sala dei Misteri' in the Grotta della Bàsura (Toirano, northern Italy) cave: An integrated morphometric and morpho-classificatory approach. *Quaternary Science Reviews* 169, 50-64.
- Coltorti M., Melis E., Patta D., 2010. Geomorphology, stratigraphy and facies analysis of some Late Pleistocene and Holocene key deposits along the coast of Sardinia. *Quaternary International* 222, 19-35.
- Comaschi Caria I., 1955a. Specie nuova di cervo nel Quaternario di Alghero. *Rendiconti del Seminario della Facoltà di Scienze dell'Università di Cagliari* 25, 182-188.
- Comaschi Caria I., 1955b. Resti di cervidi nel Quaternario di Porto Vesme (Sardegna sud-occidentale). *Rivista Italiana di Paleontologia e Stratigrafia* 61, 17-26.
- Comaschi Caria I., 1965. L'elefante nano del Quaternario di Gonnessa (Sardegna sud-occidentale). *Rendiconti del Seminario della Facoltà di Scienze Università di Cagliari* 35, 1-11.
- Comaschi Caria I., 1968. Fossili marini e continentali del Quaternario della Sardegna. *Atti del X Congresso Internazionale di Studi Sardi (Simposio sul Quaternario Sardo)*, 139-230.
- De Lorenzo G., D'Erasmus G., 1932. L'uomo paleolitico e l'*Elephas antiquus* nell'Italia meridionale. *Atti Reale Accademia di Scienze Fisiche e Matematiche di Napoli* 19, 1-106.
- De Rita D., Giordano G., Milli S., 1998. Forestepping-backstepping stacking pattern of volcanoclastic successions: Roccamonfina volcano, Italy. *Journal of Volcanology and Geothermal Research* 80, 157-178.
- Demathieu G., Ginsburg L., Guerin C., Truc G., 1984. Étude paléontologique, ichnologique et paléocéologique du gisement oligocène de Saignon (Bassin d'Apt, Vaucluse). *Bulletin du Muséum National d'Histoire Naturelle. Section C, Sciences de la terre, paléontologie, géologie, minéralogie* 6, 153-183.
- Depéret C., 1897. Etude de quelques gisements nouveaux de Vertébrés pléistocènes de l'île de Corse. *Annales de la Société Linnéenne de Lyon* 44, 111-128.
- Diedrich C.G., 2011. An Overview of the Ichnological and Ethological Studies in the Cave Bear Den in Urşilor Cave (Western Carpathians, Romania). *Ichnos* 18, 9-26.
- Di Lorenzo H., Di Vito M.A., Talamo P., Bishop J., Castaldo N., de Vita S., Nave R., Pacciarelli M., 2013. The impact of the Pomici di Avellino Plinian eruption of Vesuvius on early and middle Bronze age human settlement in Campania (Southern Italy). *Tagungen des Landesmuseums für Vorgeschichte Halle 9*, 253-265.
- Di Vito M.A., Talamo P., de Vita S., Rucco I., Zanchetta G., Cesarano M., 2019. Dynamics and effects of the Vesuvius Pomici di Avellino Plinian eruption and related phenomena on the Bronze Age landscape of Campania region (Southern Italy). *Quaternary International* 499, 231-244.
- Di Vito M.A., Talamo P., Rucco I., Di Lorenzo H., 2018. The Vesuvius Pomici di Avellino eruption and related phenomena: effects on the Bronze Age landscape of Campania Region (Southern Italy). *Alpine and Mediterranean Quaternary* 31, 205-208.
- Di Vito M.A., Zanella E., Gurioli L., Lanza R., Sulpizio R., Bishop J., Tema E., Boenzi G., Laforgia E., 2009. The Afragola settlement near Vesuvius, Italy, the destruction and abandonment of a Bronze Age village revealed by archaeology, volcanology and rock-magnetism. *Earth and Planetary Science Letters* 277, 408-421.
- Falconer H., 1857. On the species of mastodon and elephant occurring in the fossil state of Great Britain. Part II. Elephas. *The Quarterly journal of the Geological Society of London* 14, 81-84.
- Falconer H., Cautley P.T., 1847. Fauna antiqua sivalensis, being the fossil zoology of the Sewalik Hills, in the north of India. Part II. Smith Elder and Co., London.
- Fanelli F., Palombo M.R., Pillola G.L., Ibba A., 2007. Tracks and trackways of *Praemegaceros cazioti* (Depéret, 1897, Artiodactyla, Cervidae) in the Pleistocene coastal deposits from Sardinia (Western Mediterranean, Italy). *Bollettino della Società Paleontologica Italiana* 46, 47-54.
- Fondi R., 1980. Orme di microsauro nel Carbonifero superiore della Sardegna. *Memorie della Società Geologica Italiana* 20, 347-356.
- Fornós J.J., Bromley R.G., Clemmensen L.B., Rodriguez-Perea A., 2002. Tracks and trackways of Bate (Artiodactyla, Caprinae) in Pleistocene aeolianites from Mallorca (Balearic Islands, Western Mediterranean). *Palaeogeography, Palaeoclimatology, Palaeoecology* 180, 277-313.
- Ghinassi M., Fidinelli F., Magi M., Sagri M., 2013. Depositional environments of the Plio-Pleistocene Upper Valdarno Basin (Tuscany, Italy). *Italian Journal of Geosciences* 132, 33-53.
- Kim J.Y., Kim K.S., Lockley M.G., Matthews N., 2008. Hominid ichnotaxonomy: an exploration of a neglected discipline. *Ichnos* 15, 126-139.
- Kindler P., Davaud E., Strasser A., 1997. Tyrrhenian coastal deposits from Sardinia (Italy): a petrographic record of high sea levels and shifting climate belts during the last interglacial (isotopic substage 5e). *Palaeogeography, Palaeoclimatology, Palaeoecology* 133, 1-25.
- Kotsakis T., Palombo M.R., Angelone C., Melis R.T., Fanelli F., 2008. Mandriola - Capo Mannu. In: Fossil mammalian biotas of Sardinia. Fieldtrip Guide-Book, Euromam, Sardinia 16-21 September 2008, 58-64.
- Laforgia E., Boenzi G., Amato L., Bishop J., Fattore L., Stanzone M., Di Vito M.A., 2013. L'impatto delle eruzioni vulcaniche nelle aree a nord di Napoli, casi da scavi recenti. *Bollettino dell'Istituto Nazionale di Geologia e Vulcanologia* 18, 110-

- 114.
- Laforgia E., Boenzi G., Amato L., Di Vito M.A., Fattore L., Stanzione M., Viglio F., 2009. The Vesuvian “Pomici di Avellino” eruption and Early Bronze Age settlement in the middle Clanis valley. *Mediterranee* 122, 101-107, doi: 10.4000/mediterranee.3253.
- Lecca L., Carboni S., 2007. The Tyrrhenian section of San Giovanni di Sinis (Sardinia): stratigraphic record of an irregular single high stand. *Rivista Italiana di Paleontologia e Stratigrafia* 113, 509-523.
- Lucas S.G., Allen B.D., Morgan G.S., Myers R.G., Love D.W., Bustos D., 2007. Mammoth footprints from the Upper Pleistocene of the Tularosa Basin, Dona Ana County, New Mexico. *New Mexico Museum of Natural History and Science* 42, 149-154.
- Madurell-Malapeira J., Palombo M.R., Sotnikova M., 2015. *Cynotherium malatestai*, sp. nov. (Carnivora, Canidae) from the early middle Pleistocene deposits of Grotta dei Fiori (Sardinia, Western Mediterranean). *Journal of Vertebrate Paleontology* 35 (4), e943400.
- Major C.I.F., 1883. Die Tyrrhenis: Studien über geographische Verbreitung von Tieren und Pflanzen im westlich Mittelmeergebiet. *Kosmos* 13, 81-106.
- Manzi G., 2016. Humans of the Middle Pleistocene: the controversial calvarium from Ceprano (Italy) and its significance for the origin and variability of *Homo heidelbergensis*. *Quaternary International* 411, 254-261.
- Manzi G., Magri D., Milli S., Palombo M.R., Margari V., Celiberti V., Barbieri M., Barbieri M., Melis R.T., Rubini M., Ruffo M., 2010. The new chronology of the Ceprano calvarium (Italy). *Journal of Human Evolution* 59, 580-585.
- Manzi G., Magri D., Palombo M.R., 2011. Early-Middle Pleistocene environmental changes and human evolution in the Italian peninsula. *Quaternary Science Review* 30, 1420-1438.
- Marchetti L., Petti F.M., Zoboli D., Pillola G.L., 2018. Vertebrate and invertebrate trace fossils in the Late Pennsylvanian (Carboniferous) fluvio-lacustrine San Giorgio Basin (south-west Sardinia): remarks on the oldest continental ichnoassociation of Italy. *Ichnos* 25, 94-105.
- Matsukawa M., Shibata K., 2015. Review of Japanese Cenozoic (Miocene-Modern) vertebrate tracks. *Ichnos* 22, 261-290.
- McNeil P., Hills L.V., Tolman S.M., Kooyman B., 2007. Significance of latest Pleistocene tracks, trackways, and trample grounds from southern Alberta, Canada. In: Lucas S.G., Spielmann J.A., Lockley M.G. (Eds.), *Cenozoic Vertebrate Tracks and Traces*. New Mexico Museum of Natural History and Science Bulletin 42, 209-223.
- Melis R.T., Palombo M.R., Ghaleb B., Meloni S., 2016. A key site for inferring the timing of dispersal of giant deer in Sardinia, the Su Fossu de Cannas cave, Sadali, Italy. *Quaternary Research* 86, 335-347.
- Milà J., Bromley R.G., Titschack J., Theodorou G., 2007. A diverse vertebrate ichnofauna from the quaternary eolian oolite, Rhodes, Greece. In: Bromley R.G., Buatois L.A., Màngano G., Genise J.F., Melchor R.N. (Eds.), *Sediment-Organism Interactions: A Multifaceted Ichnology*. SEPM (Society for Sedimentary Geology) Special Publication 88, 333-343.
- Milà J., Theodorou G., Loope D.B., Panayides J., Clemmensen L.B., Gkioni B., 2015. Vertebrate tracks in Late Pleistocene-Early Holocene (?) carbonate aeolianites, Paphos, Cyprus. *Annales Societatis Geologorum Poloniae* 85, 507-514.
- Muñiz F., Cáceres L.M., Rodríguez-Vidal J., Neto de Carvalho C., Belo J., Finlayson C., Sugisaki S., Gómez P., Jiménez-Espejo F.J., 2019. Following the last Neanderthals, Mammal tracks in Late Pleistocene coastal dunes of Gibraltar (S Iberian Peninsula). *Quaternary Science Reviews* 217, 297-309.
- Neto de Carvalho C., 2010. Vertebrate tracksites from the Mid-Late Pleistocene eolianites of Portugal, the first record of elephant tracks in Europe. *Geological Quarterly* 53, 407-414.
- Neto de Carvalho C., 2011. Pegadas de vertebrados nos eolianitos do Pleistocénico Superior do Sudoeste Alentejano, Portugal. *Comunicações Geológicas* 98, 99-108.
- Neto de Carvalho C., Figueiredo S., Belo J., 2016. Vertebrate tracks and trackways from the pleistocene eolianites of SW Portugal. *Comunicações Geológica* 103, 101-116.
- Orain R., Lebreton V., Russo Ermolli E., Sémah A.M., Nomade S., Shao Q., Bahain J.J., Thun Hohenstein U., Peretto C., 2013. Hominin responses to environmental changes during the Middle Pleistocene in central and southern Italy. *Climate of the Past* 9, 687-697.
- Orrù P., Ulzega A., 1986. Geomorfologia costiera e sottomarina della Baia di Funtanamare (Sardegna sud-occidentale). *Geografia fisica e Dinamica Quaternaria* 9, 59-67.
- Palombo M.R., 2009. Biochronology, paleobiogeography and faunal turnover in western Mediterranean Cenozoic mammals. *Integrative Zoology* 4, 367-386.
- Palombo M.R., 2014. Deconstructing mammal dispersals and faunal dynamics in SW Europe during the Quaternary. *Quaternary Science Reviews* 96, 50-71.
- Palombo M.R., 2018a. Insular mammalian fauna dynamics and paleogeography: a lesson from the Western Mediterranean islands. *Integrative Zoology* 13, 2-20.
- Palombo M.R., 2018b. Twenty years after: Reflections on the Aurelian European Land Mammal Age. *Alpine and Mediterranean Quaternary* 31, 177-180.
- Palombo M.R., Ferretti M.P., 2005. Elephant fossil record from Italy, knowledge, problems, and perspectives. *Quaternary International* 126, 107-136.
- Palombo M.R., Giovinazzo C., 2005. *Elephas falconeri* from Spinagallo Cave (South-Eastern Sicily, Hyblean Plateau, Siracusa), brain to body weight comparison. *Monografies de la Societat d’Història Natural de les Balears* 12, 255-264.
- Palombo M.R., Rozzi R., 2014. How correct is any chronological ordering of the Quaternary Sardinian mammalian assemblages? *Quaternary International* 328, 136-155.
- Palombo M.R., Ferretti M.P., Pillola G.L., Chiappini L., 2012a. A reappraisal of the dwarfed mammoth *Mammuthus lamarmorai* (Major, 1883) from Gonnesa (south-western Sardinia, Italy). *Quaternary International* 255, 158-170.
- Palombo M.R., Gallai G., Arca M., Rook L., Tuveri C., 2012b. *Sus sondaari* van der Made, 1999 (Mammalia, Suidae) from Monte Tuttavista (Orosei, western Sardinia, Italy). *Rivista*

- Italiana di Paleontologia e Stratigrafia 118, 183-191.
- Palombo M.R., Panarello A., Mietto P., 2018. Did elephants meet humans along the Devil's Path? A Preliminary Report. *Alpine and Mediterranean Quaternary* 31, 83-87.
- Palombo M.R., Rozzi R., Bover P., 2013. The endemic bovids from Sardinia and the Balearic Islands: state of the art. *Geobios* 46, 127-142.
- Palombo M.R., Vall A.M., Arca M., Tuveri C., 2006. A new bovid, *Asoletragus gentryi* n. gen. et n. sp., from Monte Tuttavista (Orosei, Eastern Sardinia, Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 112, 1-13.
- Panarello A., Palombo M.R., Biddittu I., Di Vito M.A., Farinano G., Mietto P., 2020. On the devil's tracks, unexpected news from the Foresta ichnosite (Roccamonfina volcano, central Italy). *Journal of Quaternary Science* 35, 444-456.
- Panarello A., Santello L., Farinano G., Bennett M.R., Mietto P., 2017a. Walking along the oldest human fossil pathway (Roccamonfina volcano, Central Italy)? *Journal of Archaeological Science: Reports* 13, 476-490.
- Panarello A., Palombo M.R., Biddittu I., Mietto P., 2017b. Fifteen years along the "Devil's Trails", new data and perspectives. *Alpine and Mediterranean Quaternary* 30, 137-154.
- Panera J., Rubio-Jara S., Yravedra J., Blain H.-A., Sesé C., Pérez-González A., 2014. Manzanares Valley (Madrid, Spain): a good country for Proboscideans and Neanderthals. *Quaternary International* 326, 329-343.
- Panin N., Avram E., 1962. Noi urme de vertebrate în Miocenu Subcarpaților românești. *Studii și Cercetări de Geologie* 7, 455-484.
- Pasenko M.R., 2017. Quantitative and qualitative data of footprints produced by Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants and with a discussion of significance towards fossilized proboscidean footprints. *Quaternary International* 443, 221-227.
- Peccerillo A., 2017. Cenozoic Volcanism in the Tyrrhenian Sea Region. Springer, pp. 170.
- Pecorini G., 1954. Le dune fossili della Nurra di Alghero. *Rendiconti Accademia dei Lincei* 16, 735-741.
- Pereira A., Nomade S., Falguères C., Bahain J.J., Tombret O., Garcia T., Voinchet P., Bulgarelli G.M., Anzidei A.P., 2017. $^{40}\text{Ar}/^{39}\text{Ar}$ and ESR/U-series data for the La Polledrara di Cecanibbio archaeological site (Lazio, Italy). *Journal of Archaeological Science Reports* 15, 20-29.
- Pereira A., Nomade S., Moncel M.H., Voinchet P., Bahain J.J., Biddittu I., Falguères C., Giaccio B., Manzi G., Parenti F., Scardia G., 2018. Integrated geochronology of Acheulian sites from the southern Latium (central Italy), Insights on human-environment interaction and the technological innovations during the MIS 11-MIS 10 period. *Quaternary Science Reviews* 187, 112-129.
- Pereira A., Nomade S., Shao Q., Bahain J.J., Arzarello M., Douville E., Falguères C., Frank N., Garcia T., Lembo G., Muttillio B., Scao V., Peretto C., 2016. $^{40}\text{Ar}/^{39}\text{Ar}$ and ESR/U-series dates for Guado San Nicola, Middle Pleistocene key site at the Lower/Middle Palaeolithic transition in Italy. *Quaternary Geochronology* 36, 67-75.
- Peretto C., Arzarello M., Bahain J.J., Boulbes N., Dolo J.M., Douville E., Falguères C., Frank N., Garcia T., Lembo G., Moigne A.M., Muttillio B., Nomade S., Pereira A., Rufo M.A., Sala B., Shao Q., Thun Hohenstein U., Tessari U., Turrini M.C., Vaccaro C., 2016. The Middle Pleistocene site of Guado San Nicola (Monteroduni, Central Italy) on the Lower/Middle Palaeolithic transition. *Quaternary International* 411, 301-315.
- Peretto C., Arzarello M., Bahain J.J., Boulbes N., Douville E., Falguères C., Frank N., Garcia T., Lembo G., Moigne A.M., Muttillio B., 2014. Guado San Nicola (Monteroduni, Prov. di Isernia). *Notiziario di preistoria e protostoria* 1, 3-5.
- Pillola G.L., Zoboli D., 2017. Dwarf mammoth footprints from the Pleistocene of Gonnese (southwestern Sardinia, Italy). *Bollettino della Società Paleontologica Italiana* 56, 57-64.
- Rouchon V., Gillot P.Y., Quidelleur X., Chiesa S., Floris B., 2008. Temporal evolution of the Roccamonfina volcanic complex (Pleistocene), Central Italy. *Journal of Volcanology and Geothermal Research* 177, 500-514.
- Rozzi R., Palombo M.R., 2013. Do methods for predicting paleohabitats apply for mountain and insular fossil bovids? *Integrative Zoology* 8, 244-259.
- Santello L., 2010. Analysis of a trampled formation, the Brown Leucitic Tuff (Roccamonfina volcano, Southern Italy). Ph.D Thesis, Università di Padova, Italy.
- Sevink J., van Bergen M.J., Van Der Plicht J., Feiken H., Anastasia C., Huizinga A., 2011. Robust date for the Bronze age Avellino eruption (Somma-Vesuvius): 3945 ± 10 cal BP (1995 ± 10 cal BC). *Quaternary Science Reviews* 30, 1035-1046.
- Shoshani H., Tassy P., 2005. Proboscidean taxonomy and classification, anatomy and physiology, and ecology and behavior. *Quaternary International* 126, 5-20.
- Studiati C., 1857. Description des fossiles de la brèche osseuse de Monreale de Bonaria près de Cagliari. In: Lamarmora A., Voyage en Sardaigne, Turin, Paris 3, 651-704.
- Van der Made J., 1999. Biogeography and stratigraphy of the Mio-Pleistocene mammals of Sardinia and the description of some fossils. In: Reumer J.W.F., de Vos J. (Eds.), *Elephants have a snorkel! Papers in honour of P.Y. Sondaar*. *Deinsea* 7, 337-360.
- Van der Made J., Palombo M.R., 2006. *Megaloceros sardus* n. sp., a large deer from the Pleistocene of Sardinia. *Hellenic Journal of Geosciences* 41, 163-176.
- Vyalov O.S., 1965. Stratigrafiya Neogenovykh molass Predkarpatskovoprogriba [Stratigraphy of the Neogene molasse of the Pre Carpathianbasin]. Kiev, Naukova Dumka (Akademiya NaukUkrainskoy SSR Institut Geologii I Geokhimii GoryuchikhIskopayemykh), 165 pp.
- Vyalov O.S., 1966. Sledy zhiznedeyatel'nosti organizmov i ikhpaleontologicheskoe znachenie [Traces of living organisms and theirpaleontological significance]. Kiev, Naukova Dumka (Akademiya NaukUkrainskoy SSR Institut Geologii I Geokhimii GoryuchikhIskopayemykh), pp. 219.
- Yabe H., 1950. Three alleged occurrences of *Stegolophodon latidens* (Clift) in Japan. *Proceedings of the Japan Academy* 26, 61-65.
- Zanolli C., Martín-Torres M., Bernardini F., Boschian G., Coppa A., Dreossi D., Mancini L., de Pinillos M.M., Martín-Francés L., de Castro J.M.B., Tozzi C., 2018. The

- Middle Pleistocene (MIS 12) human dental remains from Fontana Ranuccio (Latium) and Visogliano (Friuli-Venezia Giulia), Italy. A comparative high resolution endostructural assessment. PloS one 13, e0189773.
- Zoboli D., Pillola G.L., 2016. Quaternary mammal fauna from “Surconis”, Bolotana (Sardinia, Italy). Bollettino della Società Paleontologica Italiana 55, 193-203.
- Zoboli D., Pillola G.L., 2017. Upper Pleistocene mammal assemblage from Su Concali Quarry (Samatzai, southern Sardinia, Italy). Rivista Italiana di Paleontologia e Stratigrafia 123, 243-254.
- Zoboli D., Pillola G.L., 2018. New evidences of mammal tracks from the Pleistocene of Gonnese area (southwestern Sardinia, Italy). Journal of Mediterranean Earth Sciences 10, 173-175.
- Zoboli D., Pala A., Pirellas A., Pillola G.L., 2019. Pleistocene mammals from Sa Cona Cave (Teulada, south-western Sardinia, Italy). Journal of Mediterranean Earth Sciences 11, 15-29.
- Zoboli D., Pillola G.L., Palombo M.R., 2018. The remains of *Mammuthus lamarmorai* (Major, 1883) housed in the Naturhistorisches Museum of Basel (Switzerland) and the complete “Skeleton-Puzzle”. Bollettino della Società Paleontologica Italiana 57, 45-57.